RESEARCH ARTICLE

Cortinarius subgenus *Vibratiles* (Agaricales), a new myxacioid taxon of global scope

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Abstract A major fungal lineage of myxacioid taxa is centred around *Cortinarius vibratilis*. This lineage is shown by morphological and multigene molecular phylogenetic analyses of the nrDNA ITS and LSU, as well as *rpb1* and *rpb2* genes to form a well-supported clade, here introduced as the new subgenus *C.* subg. *Vibratiles* consisting of four sections and various small clades. Two new myxacioid sections, *C.* sect. *Microspermi* and *C.* sect. *Turcopedes*, are also proposed.

Keywords bihemispherical; glutinous veil; multigene phylogeny; section rank; South Pacific; taxonomy

■ INTRODUCTION

The large genus *Cortinarius* (Pers.) Gray has traditionally been split into 4–7 subgenera, beginning with Fries (1836–1838). Since that time there have been several modifications, e.g., Kühner & Romagnesi (1953), Moser & Horak (1975), Moser (1983), Moënne-Loccoz & Reumaux (1990: 31), and Brandrud & al. (1994: 31). *Cortinarius* subg. *Myxacium* (Fr.) Trog (type: *C. collinitus* (Sowerby) Gray) has always been one of the largest subgenera with over 200 species listed in the cited works.

With the advent of molecular analyses, studies of *Cortinarius* taxonomy have shown repeatedly that most of the subgenera are polyphyletic (e.g., Peintner & al., 2004; Garnica & al., 2005; Harrower & al., 2015; Soop & al., 2019). For example, *C.* subg. *Telamonia* (Fr.) Trog has been split into a core subgenus and at least five segregate sections (Niskanen, 2008; Soop & al., 2019). Similarly, several of the *C.* subg. *Myxacium* s.l. clades were shown to be phylogenetically unrelated to *C. collinitus*, leaving the reduced *C.* subg. *Myxacium* s.str. with five main sections and about 43 species (Soop & al., 2021).

It has been evident from global studies of *Cortinarius* (Peintner & al., 2004; Garnica & al., 2016; Soop & al., 2019) that there exists a major lineage of myxacioid taxa beside *C.* subg. *Myxacium* (s.str.), which is centred around *C. vibratilis* (Fr.) Fr. Whereas the subgenus was supported by a 5-locus study (suppl. fig. S2 in Garnica & al., 2016) and by a 4-locus study (Soop & al., 2019), there has been no attempt to address the *C. vibratilis* complex with an adequate number of molecular loci. In the second cited study, this complex was described as *C.* sect. *Vibratiles* Melot, but samples in this particular clade were (with one exception) sequenced only in the nrITS and nrLSU regions.

In the present study we aim to investigate the structure of the Vibratiles lineage, using more loci. We show that the lineage can be conceived as a new subgenus in *Cortinarius*, distinct from *C.* subg. *Myxacium*. In addition, there are several myxacioid clades and sections that fall outside both lineages, which were briefly discussed in Soop & al. (2019, 2021). Even though we include many samples in the genetic dataset, these clades are here deferred to the Discussion.

■ MATERIALS AND METHODS

Taxon sampling. — All known species in the Vibratiles clade are represented in the study, as well as several myxacioid species from other groups. 239 ITS, LSU, *rpb1*, and *rpb2* sequences were selected from GenBank, and another 38 from specimens in various herbaria (mainly PDD, S, TUF, UBC) were generated in this study. Four representative species from *Cortinarius* subg. *Callistei* were chosen as outgroup. See Appendix 1 for GenBank numbers, and other data for all samples used in this study.

Molecular methods and phylogenetic reconstruction. — For a detailed description of the methods used for DNA

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extractions and PCR procedures see Soop & al. (2016), Papp & Dima (2018), Liimatainen & al. (2020), and Nilsen & al. (2021). The sequences were pre-checked and edited in MEGA v.7 (Kumar & al., 2016) or CodonCode Aligner v.9.0.1 (CodonCode, Centerville, Massachusetts, U.S.A.).

Multiple sequence alignments were generated separately on four gene regions using the online version of MAFFT v.7 (Katoh & Standley, 2013). The alignments were composed of 139 ITS, 91 LSU, 28 *rpb1*, and 19 *rpb2* sequences, respectively. They were performed with the E-INS-i algorithm (Katoh & Standley, 2013) for the ITS region, the G-INS-i algorithm (Katoh & al., 2005) for the LSU, and the FFT-NS-i algorithm (Katoh & al., 2002) for *rpb1* and *rpb2* protein-coding genes. The alignments were manually corrected and trimmed. A 4-locus alignment was generated by concatenating the ITS, LSU, *rpb1* and *rpb2* alignments in SeaView v.4 (Gouy & al., 2010). According to previous studies (e.g., Nagy & al., 2012; San-Fabian & al., 2018; Soop & al., 2019), the phylogenetically informative insertion/deletion positions (indels) in the ITS as well as the LSU alignments were coded in FastGap v.1.2 (Borchsenius, 2009) following the simple indel coding algorithm (Simmons & al., 2001). Additionally, a 2-locus alignment of ITS and LSU was also concatenated, but gaps were not coded.

The partitioned alignment of the 4-locus dataset was analysed with maximum likelihood method using raxmlGUI v.1.5.2 (Silvestro & Michalak, 2012). The GTRGAMMA substitution model for the six nucleotide partitions (ITS1 + 5.8S + ITS2 + LSU + *rpb1* + *rpb2*) and the default setting for binary (indel) data was chosen. Rapid bootstrap analysis with 1000 replicates was applied for testing branch support.

The 2-locus ITS + LSU concatenated alignment was also analysed with PhyML v.3.1 (Guindon & Gascuel, 2003) using the following settings: GTR + I + Γ model of evolution, gamma distribution of 10 rate categories, and tree topology search as SPR.

Furthermore, Bayesian inference was performed for the 2-locus dataset with MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003). The alignment was divided into four partitions (ITS1, 5.8S, ITS2, LSU) under the GTR + Γ substitution model. Two independent runs of four Markov Chain Monte Carlo (MCMC) analyses were performed each for 5 million generations, sampling every 500th generation. The first 30% of the trees were discarded as burn-in. For the remaining trees, a 50% majority-rule consensus phylogram with posterior probabilities as nodal supports was computed. The corresponding phylograms were in all cases edited and visualised in MEGA v.7 (Kumar & al., 2016) and Adobe Illustrator CS4.

In the following, to describe genetic diversity we use the notation $x(y)$ to denote the number x of nuclear substitutions, and y the number of distinct indel events in the ITS (barcode) region.

Morphology. — The new taxa at subgeneric and section rank are described in terms of the diameter of the pileus of mature specimens, hygrophanity, viscidity, lamella colour of young individuals, stipe shape, and the alkaline reaction when reported in the literature. The universal and partial veils of the basidiomata are referred to as “veil” and “cortina”, respectively. Microscopic data include spore size, shape, and ornamentation, and, where significant, cystidia size and shape, and the presence of clamp connections.

Geographical abbreviations. — The following abbreviations are used in the Taxonomy section, the table and figures: Aus (Australia), Eur (Europe), NAm/SAm/CAm (North/South/Central America), NCal (New Caledonia), NZ (New Zealand).

■ RESULTS

The aligned and trimmed regions show a varying proportion of polymorphic sites: ITS (ITS1, 5.8S, ITS2, excluding indel codes) 47%, *rpb1* 41%, *rpb2* 29%, and LSU 23%. Frøslev & al. (2005), who did not address the LSU region, found comparable proportions for the other regions. Moreover, Frøslev & al. (2005) stressed the beneficiary effect of the *rpb* regions on branch support, whereas the topology was less sensitive. The same conclusions were reached by Soop & al. (2019), who also reported a significant improvement of support when even a few *rpb* sequences were added. This appears to be the case also in our analysis, which is based on a comparatively small number of *rpb* sequences (see below).

Phylogeny. — The final 2- and 4-locus alignments are available in TreeBase (TB2:S29355). The final 4-locus alignment comprises 139 sequences and 4055 sites (including 116 binary characters), whereas the 2-locus alignment comprises 139 sequences and 1757 sites (no binary characters). The two resulting phylograms display largely the same topology. The support values of the 2-locus phylogram analysed in PhyML and MrBayes are depicted in Fig. 1, while those of the 4-locus + gap-coding phylogram analysed in RAxML are depicted in Fig. 2.

These phylograms reveal a major, well-supported clade (maximum likelihood bootstrap support = 92%/Bayesian posterior probability = 0.99 in Fig. 1, maximum likelihood bootstrap support = 83% in Fig. 2) that includes *Cortinarius* sect. *Vibratiles* together with a number of smaller sister subclades, further detailed below under Taxonomy. Remaining identified myxacioid clades, such as *C.* subg. *Myxacium*, and *C.* sect. *Delibuti*, are not closely related. This topology corroborates that found by Soop & al. (2019), but the latter authors did not explicitly name the clades. Consequently, this major clade is introduced here as the new *C.* subg. *Vibratiles*.

Taxonomy. — After submission of the present article, a major publication on Cortinariaceae taxonomy was presented (Liimatainen & al., 2022), in which the genus *Cortinarius* is replaced by 10 genera (for an informal synopsis, see Soop, 2022). With the adoption of the revised taxonomy, our new taxa *Cortinarius* subg. *Vibratiles* with its sections, and *C.* sect. *Turcopedes* would be recombined into the genus *Thaxterogaster*.

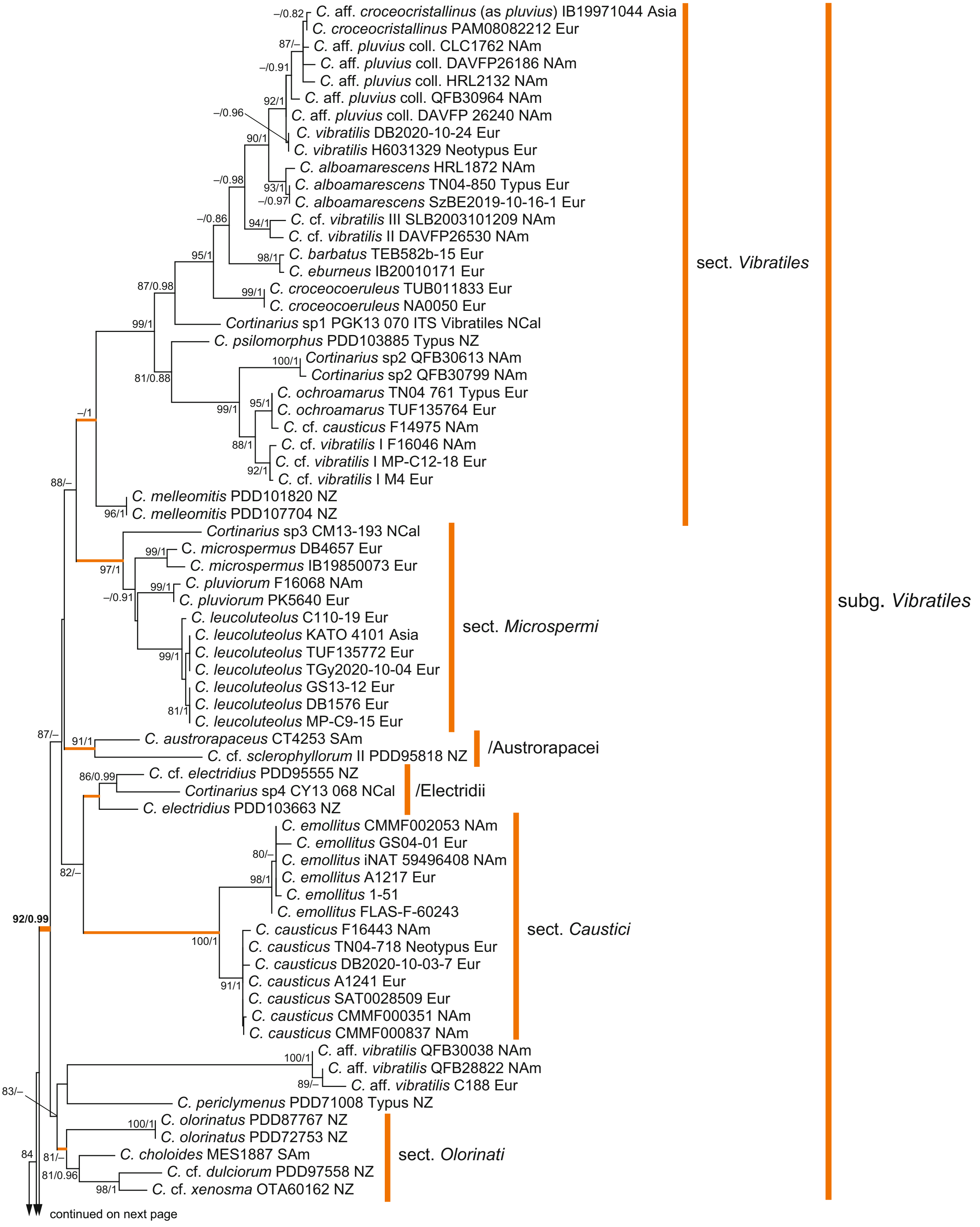

Fig. 1. Maximum likelihood (PhyML) phylogenetic tree covering the main sections of *Cortinarius* subg. *Vibratiles* subg. nov. and other myxacioid taxa based on the nrDNA ITS and LSU dataset. Support values of SH-aLRT (≥80%) followed by Bayesian posterior probabilities (>0.8) from Bayesian analysis are shown at the branches. Vertical orange bars depict *C.* subg. *Vibratiles* and the sections within. Vertical blue bar indicates the additionally described new *C.* sect. *Turcopedes* outside the subgenus. Scale bar indicates 0.01 expected changes per site per branch.

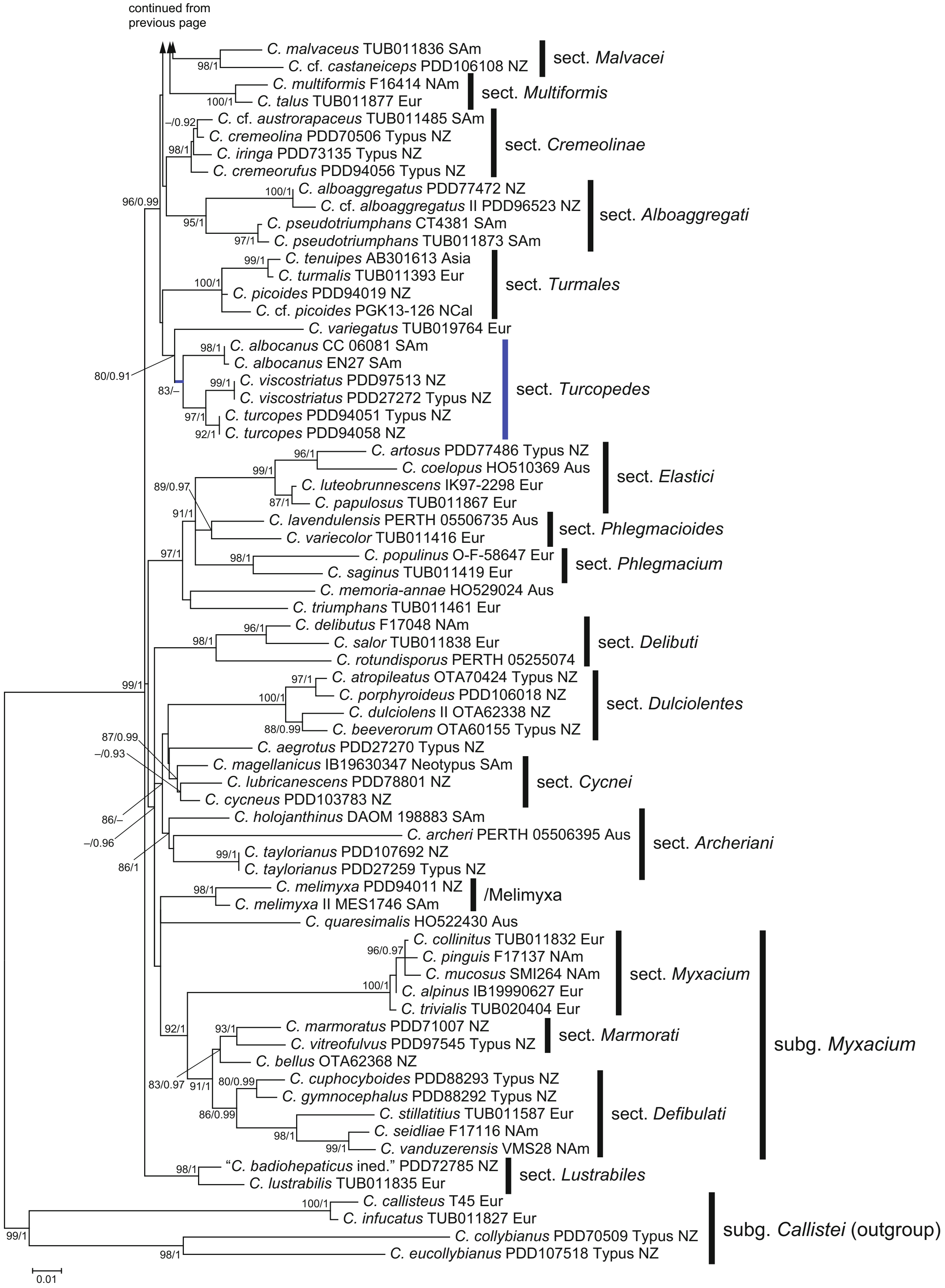

Fig. 1. Continued.

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Fig. 2. Maximum likelihood (RAxML) phylogenetic tree covering the main sections of *Cortinarius* subg. *Vibratiles* subg. nov. and other myxacioid taxa based on the 4-locus dataset with binary characters from gap coding. ML bootstrap support values (>50%) are shown at the branches. Vertical orange bars depict *C.* subg. *Vibratiles* and the sections within. Vertical blue bar indicates the additionally described new *C.* sect. *Turcopedes* outside the subgenus. Scale bar indicates 0.03 expected changes per site per branch.

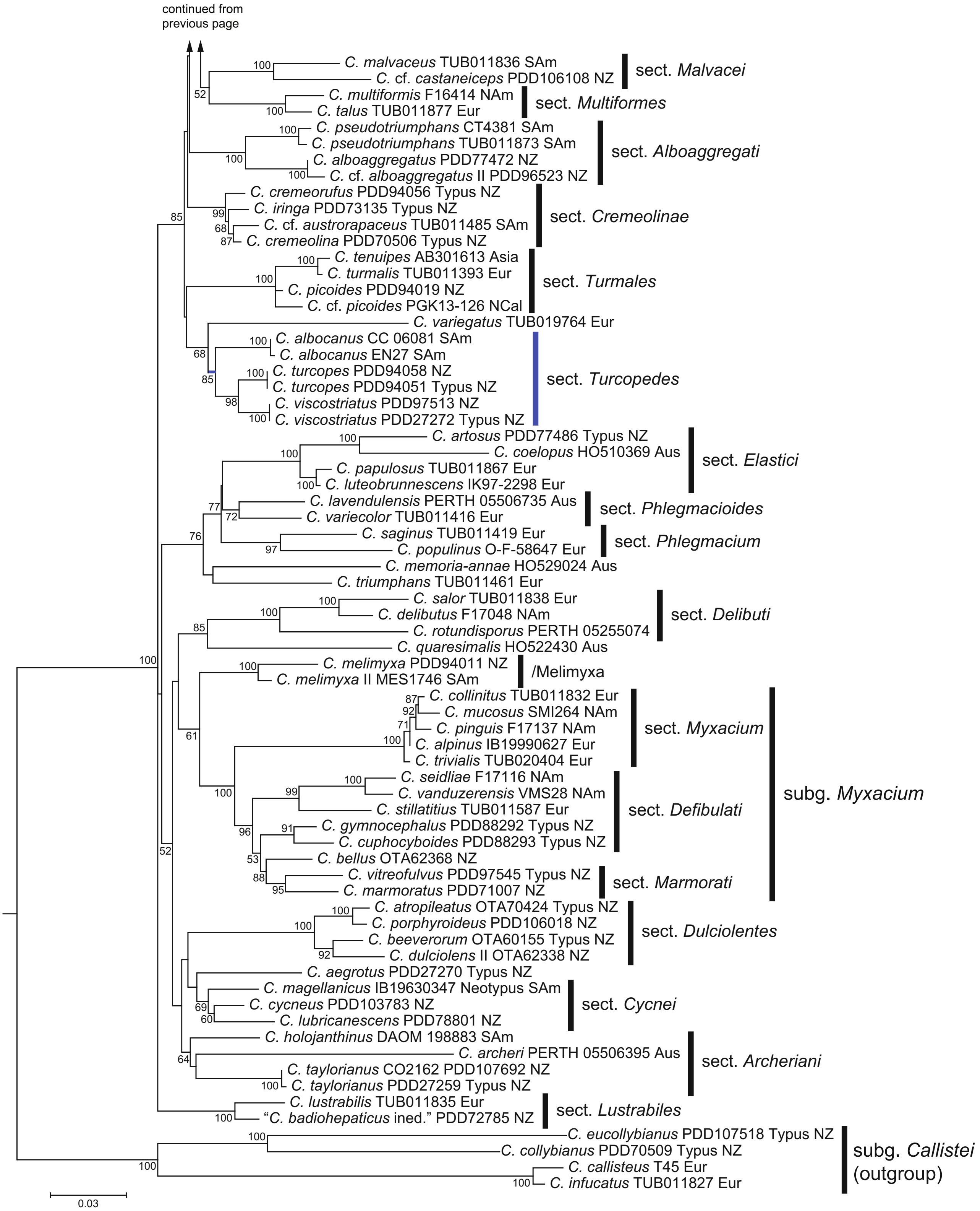

Fig. 2. Continued.

Cortinarius subg. ***Vibratiles*** Soop, Orlovich & Dima, **subg. nov.** – Type: *Cortinarius vibratilis* (Fr.) Fr. [MycoBank MB 842494].

Etymology. – After the type species *Cortinarius vibratilis* (Fig. 3A).

Description. – Habit agaricoid, small to medium sized. Pileus 15–70 mm diam., viscid to glutinous, hygrophanous or not, usually pale, whitish or yellowish, occasionally orange-brown to red-brown, violaceous only in one species, glabrous. Lamellae white to pale grey-brown when young, medium crowded to rather distant. Stipe cylindrical to slightly clavate, mostly slender, bulbous only in two species, viscid to dry, whitish. Universal veil glutinous or very sparse, hyaline, but red in two species; cortina often rudimentary. Context white to pale greyish yellow; odour insignificant, taste often bitter. Macrochemical reactions insignificant with alkaline solutions. Spores mostly ellipsoid, 6–8 (10) × 3.5–5 µm, usually weakly verrucose. Cystidia none. Clamp connections present.

Ecology. – In most types of ectomycorrhizal, temperate forests. Europe, the Americas, New Zealand, New Caledonia.

Comments. – Species in the subgenus recall those of *Cortinarius* subg. *Myxacium*, to which they have traditionally been attributed (Soop & al., 2021). Typical basidiomata differ by a smaller size, a less glutinous veil, and smaller, more ellipsoid basidiospores. A bitter taste in the context, or sometimes only in the pileal cutis, is a typical trait for many species. The type species of the subgenus, *C. vibratilis* is common and well-known in coniferous forests of the Northern Hemisphere and has recently been neotypified in Liimatainen & Niskanen (2021).

Identified members of *Cortinarius* subg. *Vibratiles*

Cortinarius sect. ***Vibratiles*** Melot in Doc. Mycol. 77: 99. 1989 – Type: *Cortinarius vibratilis* (Fr.) Fr. [MycoBank MB 701617].

= *Cortinarius* sect. *Ochroleuci* Konrad & Maubl., Les Agaricales 1 [in Encycl. Mycol. 14]: 210. 1948 – Type: *Cortinarius ochroleucus* (Schaeff.) Fr. [MycoBank: MB 845586].

Currently included species. – *Cortinarius alboamarescens* Kytöv., Niskanen & Liimat. (Eur), *C. barbatus* (Batsch) Melot (= *C. eburneus* (Velen.) Rob.Henry ex Bon) (Eur), *C. croceocoeruleus* (Pers.) Fr. (Eur), *C. melleomitis* M.M.Moser & E.Horak (SAm, NZ), *C. ochroamarus* Niskanen, Kytöv. & Liimat. (Eur), *C. psilomorphus* Soop (NZ), *C. vibratilis* (Fr.) Fr. (Eur, NAm), *C.* cf. *vibratilis* I (NAm), *C.* cf. *vibratilis* II

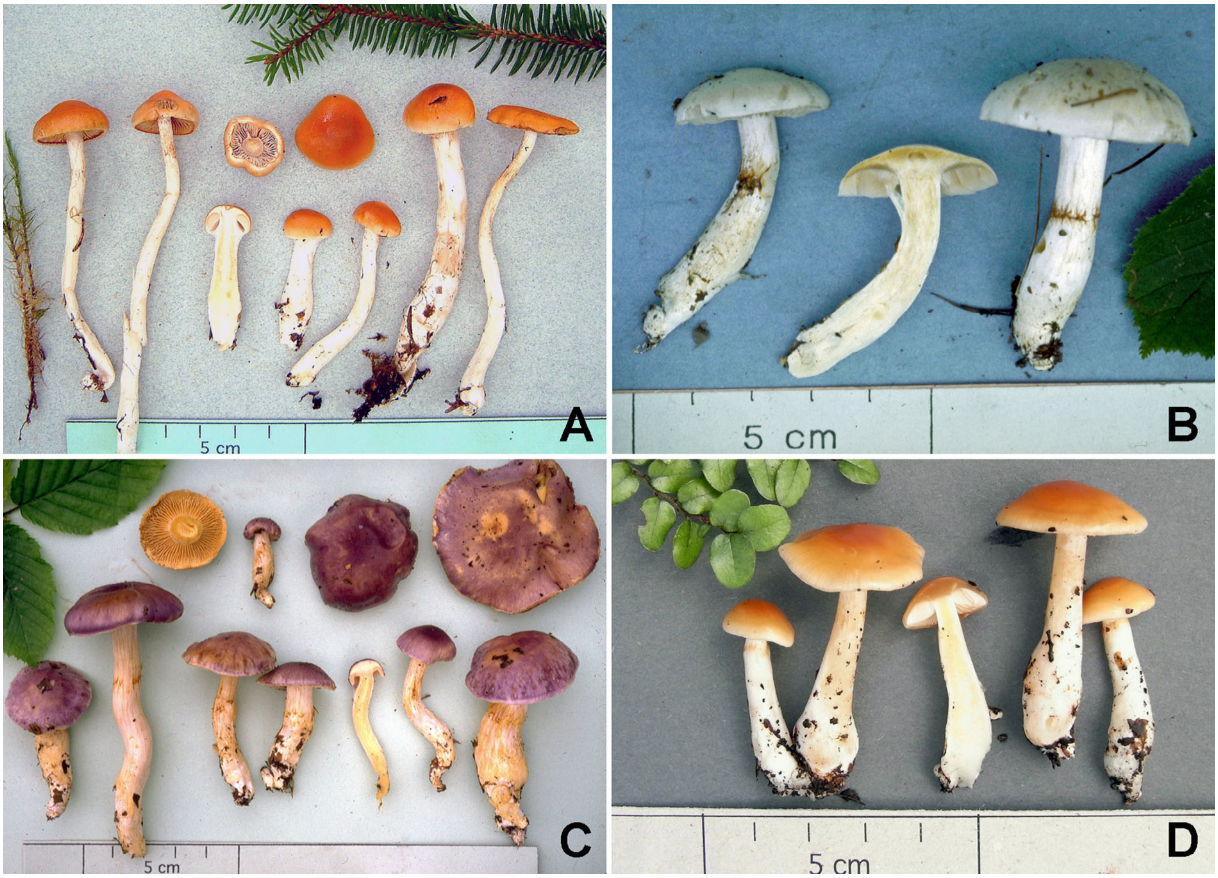

Fig. 3. Macromorphology in *Cortinarius* subg. *Vibratiles*: **A**, *C. vibratilis* (coll. KS-CO1501); **B**, *C. barbatus* (coll. KS-CO271); **C**, *C. croceocoeruleus* (coll. KS-CO987); **D**, *C. melleomitis* (coll. KS-CO1989). — Photos: K. Soop.

(NAm), *C.* cf. *vibratilis* III (NAm), *Cortinarius* sp. 1 (NCal), *Cortinarius* sp. 2 (NAm), *Cortinarius* aff. *pluvius* coll. (NAm/Eur).

Comments. – The type section of the subgenus is bihemispherical, consisting of viscid, agaricoid fungi. These are often pale with primarily white (e.g., *C. barbatus*, Fig. 3B) and yellow colours but *C. croceocoeruleus* (Fig. 3C) deviates by its violaceous pileus. Many species have a bitter taste.

Cortinarius sect. *Vibratiles*, as it was conceived in Soop & al. (2019), circumscribed several clades that are here broken out as segregate entities. *Cortinarius* sect. *Ochroleuci* has partly the same species content (Moser in Singer, 1986), but since no genetic data of its type *C. ochroleucus* is available, it is currently not possible to clarify its relation to the present section.

In our phylograms (Figs. 1, 2), the crown clade including *Cortinarius vibratilis* s.str. and sequences labelled as *C. pluvius* and *C. croceocristallinus* form a well-defined clade with a maximum genetic diversity of 12(5) (see Methods), yet with an ecological heterogeneity in that both conifers and *Alnus* are among the host plants. We distinguish a subclade containing the neotype of *C. vibratilis*, but delimiting other species in the clade is more problematic, as neither a neotype of the Friesian *C. pluvius* has been proposed nor is any reference sequence currently available for *C. croceocristallinus*. Current interpretations of *C. pluvius* (e.g., Brandrud & al., 1998) suggest a species from coniferous forests with a morphology similar to that of *C. vibratilis*, possibly with more yellow colour tones. Based on these considerations, we currently regard *C. pluvius* as a nomen dubium and the samples so labelled in this clade as *C.* aff. *pluvius* coll. or *C.* aff. *croceocristallinus*.

Cortinarius melleomitis was originally described from Patagonia in *C.* subg. *Myxacium* by Moser & Horak (1975) but was later moved to *C.* subg. *Paramyxacium* by Horak & Wood (1990), who also included findings from New Zealand. No holotype sequences have been available, and we have so far only examined material from New Zealand (Fig. 3D). The fungus has a strong resemblance to *C. pluvius* and other northern species in *C.* sect. *Vibratiles* but is not bitter in taste (*inde nomen*). Even if it is not strongly supported in all phylograms, we tentatively treat *C. melleomitis* as a member, rather than a sister species, of *C.* sect. *Vibratiles* due to its conforming morphology.

Cortinarius sect. ***Caustici*** Niskanen & Liimat., Index Fung. 477: 1. 2021 – Type (designated by Niskanen & Liimatainen in Index Fungorum 477: 1. 2021): *Cortinarius causticus* Fr. [Index Fungorum IF 558173].

Currently included species. – *Cortinarius causticus* Fr. (Eur, NAm) (Fig. 4C), *C. emollitus* Fr. (Eur).

Comments. – A small northern clade of pale, glutinous fungi resembling those in the preceding sections. The *Cortinarius emollitus* clade has a maximum intraspecific ITS diversity of 4(1).

Cortinarius sect. ***Microspermi*** Soop, Orlovich & Dima, **sect. nov.** – Type: *Cortinarius microspermus* J.E.Lange [MycoBank MB 842620].

Description. – Habit agaricoid. Pileus 15–75 mm diam., viscid to almost dry, mostly hygrophanous, pale greyish, yellowish, or red-brown, glabrous to pruinose. Lamellae white to pale grey when young, medium crowded. Stipe cylindrical to slightly clavate, slender, viscid to dry, whitish. Veil sparse, white; cortina often rudimentary. Context white to pale yellow; odour insignificant, taste mild to slightly bitter. Macrochemical reactions insignificant with alkaline solutions. Basidiospores ellipsoid, 4–8 × 3.5–4.5 µm, weakly verrucose. Figure 4A,B.

Ecology. – In *Picea*, *Pinus*, and broad-leaf forests. Europe, North America, and the South Pacific.

Currently included species. – *Cortinarius leucoluteolus* Rob.Henry (= *C. emollitoides* Bidaud, Moënne-Locc. & Reumaux) (Eur) (Fig. 4A), *C. microspermus* J.E.Lange (Eur) (Fig. 4B), *C. pluviorum* Jul.Schäff. ex M.M.Moser (Eur), *Cortinarius* sp. 3 (NCal).

Comments. – A largely northerly section of fungi that resemble those in *Cortinarius* sect. *Vibratiles*, but typically produce smaller basidiospores and their taste is not strongly bitter. *Cortinarius galeobdolon* is likely a synonym of *C. leucoluteolus*, but the type of the first has not been available for sequencing and comparison so far.

Cortinarius sect. ***Olorinati*** Soop & Dima in Phytotaxa 438 (4): 232. 2020 – Type: *Cortinarius olorinatus* E.Horak [MycoBank MB 833327].

Comments. – The section is so far confined to the Southern Hemisphere. Its members are medium-sized (pilei 25–40 mm diam.), generally pale and viscid, fruiting under *Nothofagus*. See Dima & Soop (2020) for details.

Clade /Austrorapacei

Currently included species. – *Cortinarius austrorapaceus* Soop & M.Wallace (SAm), *C.* cf. *sclerophyllorum* (NZ).

Comments. – A small southern clade of agaricoid species, consistently present in all our trees but with low support. Several collections labelled *Cortinarius rapaceus* var. *luridus*, the basionym of *C. austrorapaceus*, have been made in South America. After genetic comparison with the holotype, it was shown by Salgado Salomón & al. (2018) that these collections represent a different species which nests in *C.* sect. *Cremeolinae*. As shown by the present study (Figs. 1, 2), *C. austrorapaceus* nests in *C.* subg. *Vibratiles*. It differs morphologically from most species in the subgenus by a phlegmacioid habit with a bulbous stipe, a trait which is, however, shared with at least two species in *C.* sect. *Olorinati* (Dima & Soop, 2020). The second species in the clade, *C.* cf. *sclerophyllorum*, is provided with a reddish veil.

Clade /Electridii

Currently included species. – "*Cortinarius electridius* ined." (NZ), "*C.* cf. *electridius* ined." (NZ), *Cortinarius* sp. 4 (NCal).

Comments. – A southern clade of small, glutinous fungi. "*Cortinarius electridius*" has a strongly bitter context.

Singleton species

Cortinarius periclymenus Soop (NZ), *C.* aff. *vibratilis* (Eur).

Comments. – These species are viscid, but not strongly so. The pileus is brownish except for *Cortinarius periclymenus*, which is a pale fungus with a strikingly red veil (Fig. 4D).

New myxacioid taxon outside *Cortinarius* subg. *Vibratiles*

Cortinarius sect. ***Turcopedes*** Soop, Orlovich & Dima, **sect. nov.** – Type: *Cortinarius turcopes* Soop [MycoBank MB 842640].

Description. – Habit agaricoid or sequestrate. Pileus 15–70 mm diam., viscid, hygrophanous or not, pale grey-brown, to olive green, glabrous, margin striate in one species. Lamellae pale argillaceous to violet when young, crowded, sinuous-curly in one species. Stipe cylindrical, bulbous in one species, viscid to dry, white to turquoise blue. Veil sparse, hyaline to violaceous; cortina often rudimentary. Context whitish to bluish; odour and taste insignificant. Macrochemical reactions insignificant or indistinctly reddish with alkaline solutions. Spores ellipsoid to amygdaloid, 8–12 × 5–6 µm, weakly verrucose. Figure 4E.

Ecology. – In *Nothofagus* forests. South America and New Zealand.

Currently included species. – *Cortinarius albocanus* (E.Horak & M.M.Moser) Peintner & M.M.Moser (SAm), *C. turcopes* Soop (NZ), *C. viscostriatus* E.Horak (NZ) (Fig. 4E).

Comments. – This myxacioid section, recovered as the clade /Turcopedes in Soop & al. (2019), is genetically well separated from *Cortinarius* subg. *Vibratiles*. *Cortinarius viscostriatus* was originally placed in *C.* subg. *Paramyxacium* (Horak & Wood, 1990). It was described from a single collection as having generally drab, greyish hues, but a turquoise blue and greenish form has subsequently been found (Fig. 4E), recalling the colours of the section type. *Cortinarius albocanus* is sequestrate (Nouhra & al., 2021) but could be regarded as "semi-agaricoid" with wavy and anastomosed lamellae. It was originally placed in the genus *Thaxterogaster* (Horak & Moser, 1965).

Fig. 4. Macromorphology in *Cortinarius* subg. *Vibratiles*: **A**, *C. leucoluteolus* (coll. KS-CO697); **B**, *C. microspermus* (coll. KS-CO230); **C**, *C. causticus* (coll. KS-CO2268); **D**, *C. periclymenus* (coll. KS-CO1232); and *C.* sect. *Turcopedes*: **E**, *C. viscostriatus* (coll. KS-CO1885). — Scale bars in C, D, and E represent 20 mm. — Photos: K. Soop.

Table 1. Summary of pre- and post-molecular placement of selected myxacioid species ordered according to post-molecular placement but prior to the systematics proposed by Liimatainen & al. (2022).

Species	Pre-molecular placement			Post-molecular placement			Provenance
Cortinarius	Subgenus	Section	Ref.	Subgenus	Section/clade	Ref.	
absinthiacus	*Myxacium*	*Cystidiferi*	MS	–	–	S19	SAm
aegrotus	*Paramyxacium*	–	HW	–	–	(S21)	NZ
aerugineoconicus	*Myxacium*	–	HW	*Phlegmacium*	*Entheosi*	S19	NZ
alienatus	*Dermocybe*	–	H88	–	–	(S19)	NZ
archeri	*Myxacium*	*Archeriani*	MS	–	*Archeriani*	S19	Aus
austrorapaceus	*Phlegmacium*	–	MH	*Vibratiles*	/Austrorapacei	pw	SAm
bellus	*Myxacium*	–	HW	*Myxacium*	–	S21	NZ
caelicolor	*Paramyxacium*	*Archeriani*	MH	–	–	(S21)	SAm
cardinalis	*Dermocybe*	–	H88	–	–	(S19)	NZ
castaneodiscus	*Dermocybe*	–	H88	–	*Ignelli*	S19	NZ
causticus	*Myxacium*	*Vibratiles*	FN	*Vibratiles*	*Caustici*	pw	Eur
choloides	*Phlegmacium*	–	H79	*Vibratiles*	*Olorinati*	DS	SAm
collinitus	*Myxacium*	*Myxacium*	MS	*Myxacium*	*Myxacium*	(S21)	Eur, NAm
columbinus	*Myxacium*	*Archeriani*	MH	–	*Cretaces*	–	SAm
cycneus	*Myxacium*	–	HW	–	*Cycnei*	S19	NZ
delibutus	*Myxacium*	*Delibuti*	FN	–	*Delibuti*	S19	Eur, NAm
emollitoides	*Myxacium*	*Vibratiles*	FN	*Vibratiles*	*Microspermi*	pw	Eur
emollitus	*Myxacium*	*Vibratiles*	MS	*Vibratiles*	*Caustici*	pw	Eur
emunctus	*Myxacium*	*Delibuti*	FN	–	–	(S19)	Eur
erythraeus	*Myxacium*	*Pyromyxa*	MS	–	*Sinapicolores*	S21	Aus
fuligineoviolaceus	*Myxacium*	*Myxacium*	MS	*Myxacium*	–	S21	SAm
gymnocephalus	*Myxacium*	*Defibulati*	GS	*Myxacium*	*Defibulati*	S19	NZ
ignotus	*Myxacium*	–	HW	–	*Sinapicolores*	S21	NZ
illitus	*Myxacium*	*Cystidiferi*	MS	–	*Delibuti*	S19	SAm
indolicus	*Myxacium*	–	HW	–	–	(S19)	NZ
ixomolynus	*Myxacium*	–	S13	–	–	(S19)	NZ
lustrabilis	*Myxacium*	*Vibratiles*	FN	–	*Lustrabiles*	S19	Eur
magellanicus	*Myxacium*	*Archeriani*	MS	–	*Cycnei*	S19	SAm
malvaceus	*Myxacium*	*Malvacei*	MH	–	*Malvacei*	S19	SAm
marmoratus	*Myxacium*	–	HW	*Myxacium*	*Marmorati*	S19	NZ
melimyxa	*Paramyxacium*	–	HW	–	–	(S21)	Aus, NZ
melleomitis	*Paramyxacium*	*Paramyxacium*	MH	*Vibratiles*	*Vibratiles*	pw	SAm, NZ
microspermus	*Myxacium*	*Vibratiles*	FN	*Vibratiles*	*Microspermi*	pw	Eur
oblongisporus	*Quadrispora*	–	BC	*Myxacium*	*Quadrispora*	S21	Aus
olivaceoniger	*Dermocybe*	–	H88	–	*Walkeri*	S19	NZ
olorinatus	*Myxacium*	–	HW	*Vibratiles*	*Olorinati*	DS	NZ
paradoxus	*Paramyxacium*	*Paramyxacium*	MS	–	*Paramyxacium*	S21	SAm
pectochelis	*Myxacium*	–	GS	–	–	(S19)	NZ
periclymenus	*Telamonia*	*Myxotelamonia*	S01	*Vibratiles*	–	pw	NZ
piriformis	*Thaxterogaster*	*Violacei*	HM	*Myxacium*	*Quadrispora*	S21	Aus

(Continues)

Table 1. Continued.

Species *Cortinarius*	Pre-molecular placement			Post-molecular placement			Provenance
	Subgenus	Section	Ref.	Subgenus	Section/clade	Ref.	
porphyrophaeus	*Myxacium*	*Pyromyxa*	MS	–	*Sinapicolores*	S21	NZ
psilomorphus	*Paramyxacium*	–	S16	*Vibratiles*	*Vibratiles*	pw	Eur, NAm
quaresimalis	*Phlegmacium*	*Delibuti*	G07	–	–	(S19)	Aus
rotundisporus	*Myxacium*	*Delibuti*	HW	–	*Delibuti*	(S19)	Aus, NZ
salor	*Myxacium*	*Archeriani*	MS	–	*Delibuti*	(S19)	Eur
semiamictus	*Paramyxacium*	*Archeriani*	MH	–	–	S21	SAm
sinapicolor	*Myxacium*	*Pyromyxa*	MS	–	*Sinapicolores*	S21	Aus
stillatitius	*Myxacium*	*Defibulati*	FN	*Myxacium*	*Defibulati*	S19	Eur, NAm
taylorianus	*Myxacium*	–	HW	–	*Archeriani*	S21	NZ
togularis	*Paramyxacium*	–	MH	–	*Purpurelli*	S19	SAm
vibratilis	*Myxacium*	*Vibratiles*	FN	*Vibratiles*	*Vibratiles*	pw	Eur, NAm
viscilaetus	*Myxacium*	–	S01	–	*Limonii*	S19	NZ
viscostriatus	*Paramyxacium*	–	HW	–	*Turcopedes*	pw	NZ
viscoviridis	*Myxacium*	–	HW	–	–	(S19)	NZ
vitreopallidus	*Myxacium*	*Marmorati*	S21	*Myxacium*	*Marmorati*	S21	NZ
vitreopileatus	*Paramyxacium*	–	HW	*Myxacium*	*Marmorati*	S19	NZ

Reference abbreviations: BC = Bougher & Castellano (1993), DS = Dima & Soop (2020), FN = *Funga Nordica*, Knudsen & Vesterholt (2012), G07 = Gasparini (2007), GS = Gasparini & Soop (2008), H79 = Horak (1979), H88 = Horak (1988), HM = Horak & Moser (1965), HW = Horak & Wood (1990), MH = Moser & Horak (1975), MS = Moser in Singer (1986), S01 = Soop (2001), S13 = Soop (2013), S16 = Soop (2016), S19 = Soop & al. (2019), S21 = Soop & al. (2021), pw = present work; "–" = no infrageneric taxon has been assigned, "(…)" = used in the analysis, but without comments.

■ DISCUSSION

Distribution. — *Cortinarius* subg. *Vibratiles* is widely distributed globally. In this study, we identify 34 species, though only 18 of them have been published. The species are evenly shared between the two hemispheres, and several are common, such as *C. vibratilis* in the coniferous forests of the North, and *C. melleomitis* and *C. periclymenus* found under *Nothofagus* in the South Pacific. Also, the other major myxacioid groups of *Cortinarius*, *C.* subg. *Myxacium* and *C.* sect. *Delibuti*, are widely distributed.

Morphology. — Basidiomata of *Cortinarius* subg. *Vibratiles* can be distinguished from those of *C.* subg. *Myxacium* by a few morphological characters, such as smaller spores and often a bitter taste (see Taxonomy). Moreover, unlike the latter, the new subgenus does not so far contain any sequestrate species. A few species in *C.* sect. *Cycnei* may recall those of *C.* subg. *Vibratiles*, such as *C. cycneus* (which resembles *C. olorinatus*). Species in *C.* sect. *Delibuti* can usually be recognised by the subglobose spores and a yellowish universal veil.

Several *Cortinarius* subg. *Vibratiles* species are of a modest stature and often distinctly hygrophanous, for example *C. pluviorum*, *C. periclymenus*, and *C. electridius*. A few Patagonian taxa with these features were assigned to *C.* sect. *Myxotelamonia* in *C.* subg. *Telamonia* s.l. (Moser & Horak, 1975), but have not been studied in the present work as no molecular data were available.

Phylogenetics. — *Cortinarius* subg. *Vibratiles* forms a robustly supported clade, well separated from *C.* subg. *Myxacium* (Fig. 1). It is also distinct from other myxacioid clades, such as *C.* sect. *Delibuti*, sect. *Cycnei*, sect. *Archeriani*, sect. *Turcopedes*, and sect. *Malvacei*. Some of these taxa were briefly discussed in Soop & al. (2021), but none has yet been assigned to a monophyletic subgenus. The same is true for numerous singleton species, almost all from the Southern Hemisphere. The only northern species not belonging to any of these groups is *C. lustrabilis*. It resembles members of *C.* sect. *Vibratiles*, but has been shown to nest in a small, isolated, bihemispherical clade (Soop & al., 2019) that was formally described as *C.* sect. *Lustrabiles* (Niskanen & Liimatainen, 2021).

Status of *Cortinarius* subg. *Myxacium* s.l. — Reviewing taxa that were either explicitly attributed to *Cortinarius* subg. *Myxacium* by their authors or described with myxacioid traits, one finds a varied mixture of groups and lineages. Of special interest are certain species from the South Pacific with a viscid universal veil and distinguished by their bright colours in the red-orange-yellow range, suggesting the presence of anthraquinonic pigments (Stensrud & al., 2014) as confirmed by a positive (usually red) alkaline reaction. Examples are taxa in *C.* sect. *Sinapicolores* (Soop & al., 2019). Others were originally described in subgenus (or genus) *Dermocybe*, such as

C. cardinalis, *C. alienatus*, and members of *C.* sect. *Walkeri* and sect. *Ignelli* (Horak, 1988). These are all closely related to non-viscid dermocyboid taxa (Soop & al., 2019).

Among other southern myxacioid taxa, one notes *Cortinarius* subg. *Paramyxacium*, originally described from South America (Moser & Horak, 1975). It was shown (Soop & al., 2019) that the type, *C. paradoxus*, nests in a clade populated by *C.* sect. *Rozites* and related rozitoid taxa. *Cortinarius togularis*, another *C.* subg. *Paramyxacium* species, was synonymised by Horak (1981) with *C. sarmienti*, a rozitoid species in *C.* sect. *Purpurelli* (Soop & al., 2019). In addition, a number of *C.* subg. *Paramyxacium* species from the South Pacific were described by Horak & Wood (1990). Among these, according to the present study (Figs. 1, 2), *C. melleomitis* belongs to *C.* subg. *Vibratiles*, *C. viscostriatus* to *C.* sect. *Turcopedes*, *C. vitreopileatus* to *C.* subg. *Myxacium*, whereas *C. melimyxa* and *C. aegrotus* are singletons.

In conclusion, the phylogeny of the myxacioid species of the world is complex and far from fully explored. In this study, we attempt to elucidate the relationships within one of the dominant groups, identified as a new subgenus. Table 1 seeks to summarise the earlier and current status of myxacioid species as known today.

■ AUTHOR CONTRIBUTIONS

KS designed the research conception. All authors contributed to the discussions, the preparation of material and the gathering of morphological, ecological and sequence data. ARN, DAO and BD performed molecular work. BD and KS performed phylogenetic analyses. KS and BD wrote the majority of the paper, prepared figures and tables. All authors interpreted the results, read and commented the manuscript several times and approved the final version. — KS, https://orcid.org/0000-0002-6888-5808; ARN, https://orcid.org/0000-0003-4724-6289; DAO, https://orcid.org/0000-0002-9266-2188; JFA, https://orcid.org/0000-0002-5121-9665; BD, https://orcid.org/0000-0003-2099-3903

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Appendix 1. Samples used in the phylogenetic analyses.

Cortinarius species, section/clade, provenance, voucher, ITS, LSU, *rpb1*, *rpb2*. Newly generated sequences are in boldface.

C. aegrotus E.Horak, –, New Zealand, PDD27270 [holotype], GU233333, GU233389, –, –; ***C. alboaggregatus*** Soop, *Alboaggregati*, New Zealand, PDD77472, AY669620, in ITS, –, –; ***C.*** cf. ***alboaggregatus*** II, *Alboaggregati*, New Zealand, PDD96523, MH101554, MH108393, MH141038, –; ***C. alboamarescens*** Kytöv., Niskanen & Liimat., *Vibratiles*, Hungary, SzBE-20191016-1, **ON832629**, –, –, –; ***C. alboamarescens***, *Vibratiles*, Finland, TN04-850 [holotype], KR011136, –, –, –; ***C. alboamarescens***, *Vibratiles*, Canada, MQ18081-HRL1872, MN750950, **ON844108**, –, **ON843890**; ***C. albocanus*** (E.Horak & M.M. Moser) Peintner & M.M.Moser, *Turcopedes*, Argentina, CORDC00006081, MG554214, –, –, –; ***C. albocanus***, *Turcopedes*, Argentina, EN27, JX983156, –, –, –; ***C. alpinus*** Boud., *Myxacium*, Austria, IB19990627, AF325575, –, –, –; ***C. archeri*** Berk., *Archeriani*, Australia, PERTH 05506395, AY669610, in ITS, –, –; ***C. artosus*** Soop, *Elastici*, New Zealand, PDD77486 [holotype], AY669644, in ITS, –, –; ***C. atropileatus*** A.R.Nilsen & Orlovich, *Dulciolentes*, New Zealand, OTA70424 [holotype], MG367632, MN492670, –, MG367646; ***C. austrorapaceus*** Soop & M.Wallace, Austrorapacei, Chile, CT4253, KY462307, –, –, –; ***C.*** cf. ***austrorapaceus***, *Cremeolinae*, Chile, TUB011485, AF539724, in ITS, –, –; "***C. badiohepaticus*** ined.", *Lustrabiles*, New Zealand, PDD72785, MH101530, MH108364, –, –; ***C. barbatus*** (Batsch) Melot, *Vibratiles*, Russia, TEB582b-15, MK358085, –, –, –; ***C. beeverorum*** Orlovich, X.Yue Wang & T.Lebel, *Dulciolentes*, New Zealand, OTA60155 [holotype], KC520546, MN492671, –, –; ***C. bellus*** E.Horak, –, New Zealand, OTA62368, KT334138, KT334148, –, KT334156; ***C. callisteus*** (Fr.) Fr., *Callistei*, Norway, T45, KC842435, KC842505, –, –; ***C.*** cf. ***castaneiceps***, *Malvacei*, New Zealand, PDD106108, MH101580, MH108418, –, –; ***C. causticus*** Fr., *Caustici*, Canada, CMMF000351, MN751068, **ON832645**, –, –; ***C. causticus***, *Caustici*, Canada, CMMF000837, MN751067, –, –, –; ***C. causticus***, *Caustici*, Hungary, DB2020-10-03-7, **ON832631**, **ON832644**, **ON843885**, –; ***C. causticus***, *Caustici*, Canada, F16443, FJ039664, in ITS, –, –; ***C. causticus***, *Caustici*, U.S.A., SAT0028509, FJ717507, in ITS, –, –; ***C. causticus***, *Caustici*, Finland, TN04-718 [neotype], MW599263, –, –, –; ***C. causticus***, *Vibratiles*, Hungary, DB2019-10-23-1, **ON832630**, –, –, –; ***C.*** cf. ***causticus***, *Vibratiles*, Canada, F14975, FJ157016, in ITS, –, –; ***C. choloides*** E.Horak, *Olorinati*, Argentina, MES1887, KY462607, –, –, –; ***C. coelopus*** Gasparini, *Elastici*, Australia, HO510369, AY669640, in ITS, –, –; ***C. collinitus*** (Sowerby) Gray, *Myxacium*, Germany, TUB011832, AY669588, in ITS, KJ403768, –; ***C. collybianus*** Soop, *Collybiani*, New Zealand, PDD70509 [holotype], GU233346, GU233417, –, MH141024; ***C. cremeolina*** Soop, *Cremeolinae*, New Zealand, PDD70506 [holotype], JX000351, JX000380, –, –; ***C. cremeorufus*** Soop, *Cremeolinae*, New Zealand, PDD94056 [holotype], KU136439, KU136441, –, –; ***C. croceocoeruleus*** (Pers.) Fr., *Vibratiles*, Hungary, NA-0050, **ON832633**, **ON832646**, **ON843886**, –; ***C. croceocoeruleus***, *Vibratiles*, Germany, TUB011833, AY669590, in ITS, –, –; ***C. croceocristallinus*** Rob.Henry, *Vibratiles*, France, PAM08082212, JQ749630, –, –, –; ***C.*** aff. ***croceocristallinus***, *Vibratiles*, Russia, IB19971044, UDB001058, –, –, –; ***C. cuphocyboides*** Soop, *Defibulati*, New Zealand, PDD88293 [holotype], AY669625, in ITS, –, –; ***C. cycneus*** E.Horak, *Cycnei*, New Zealand, PDD103783, MH101565, MH108403, –, –; ***C. delibutus*** Fr., *Delibuti*, Canada, F17048, FJ717515, in ITS, –, –; ***C. dulciolens*** II, *Dulciolentes*, New Zealand, OTA62338, KF977697, MN841772, –, MG367647; ***C.*** cf. ***dulciorum***, *Olorinati*, New Zealand, PDD97558, KJ635246, in ITS, –, –; ***C. eburneus*** (Velen.) Rob.Henry ex Bon, *Vibratiles*, Italy, IB20010171, UDB001101, –, –, –; "***C. electridius*** ined.", Electridii, New Zealand, PDD103663, KF727373, KF727329, MZ727578, MZ727573; ***C.*** cf. "***electridius***", Electridii, New Zealand, PDD95555, MW263666, –, –, –; ***C. emollitus*** Fr., *Caustici*, Hungary, DB2019-09-01-1, **ON832638**, –, –, –; ***C. emollitus***, *Caustici*, Canada, CMMF002053, MN751078, **ON832647**, –, –; ***C. emollitus***, *Caustici*, Germany, GS04-01, **ON832639**, –, –, –; ***C. emollitus***, *Caustici*, U.S.A., iNAT-59496408, MW031158, –, –, –; ***C. emollitus***, *Caustici*, Poland, 1-51, HQ115589, –, –, –; ***C. emollitus***, *Caustici*, U.S.A., FLAS -F-60243, MH108577, –, –, –; ***C. eucollybianus*** Soop, *Collybiani*, New Zealand, PDD107518 [holotype], MF568046, MF568051, –, –; ***C. gymnocephalus*** Soop, *Defibulati*, New Zealand, PDD88292 [holotype], AY669629, in ITS, –, –; ***C. holojanthinus*** Peintner & M.M.Moser, *Archeriani*, Argentina, DAOM198883, AF325556, AF261552, –, –; ***C. infucatus*** Fr., *Callistei*, Germany, TUB011827, AY669594, in ITS, KJ403785, –; ***C. iringa*** Soop, *Cremeolinae*, New Zealand, PDD73135 [holotype], EU660948, in ITS, –, –; ***C. lavendulensis*** Cleland, *Phlegmacioides*, Australia, PERTH 05506735, AY669617, in ITS, –, –; ***C. leucoluteolus*** Rob.Henry, *Microspermi*, Germany, GS13-12, **ON832634**, –, –, –; ***C. leucoluteolus***, *Microspermi*, Turkey, KATO Fungi 4101, MT367147, –, –, –; ***C. leucoluteolus***, *Microspermi*, Hungary, TGy20201004, **ON832635**, –, –, –; ***C. leucoluteolus***, *Microspermi*, Hungary, DB1576, MK358091, –, –, –; ***C. leucoluteolus***, *Microspermi*, Norway, MP-C9-15, **ON832637**, –, –, –; ***C. leucoluteolus***, *Microspermi*, Norway, C110-19, **ON832636**, –, –, –; ***C. leucoluteolus***, *Microspermi*, Germany, TUF135772, UDB0799943, –, –, –; ***C. lubricanescens*** Soop, *Cycnei*, New Zealand, PDD78801, KJ421073, in ITS, KJ403770, –; ***C. lustrabilis*** Moënne-Locc., *Lustrabiles*, Germany, TUB011835, AY669586, in ITS, KJ403766, –; ***C. luteobrunnescens*** A.H.Sm., *Elastici*, Finland, IK97-2298, KF732620, –, –, –; ***C. magellanicus*** Speg., *Cycnei*, Chile, IB19630347 [neotype], AF389125, AF388758, –, –; ***C. malvaceus*** E.Horak, *Malvacei*, Chile, TUB011836, AY669611, in ITS, KJ403801, –; ***C. marmoratus*** E.Horak, *Marmorati*, New Zealand, PDD71007, GU233350, GU233381, –, –; ***C. melimyxa*** E.Horak, Melimyxa, New Zealand, PDD94011, GU233369, –, –, –; ***C. melimyxa*** II, Melimyxa, Chile, MES1746, KY462542, –, –, –; ***C. melleomitis*** M.M.Moser & E.Horak, –, New Zealand, PDD101820, KJ635206, in ITS, –, –; ***C. melleomitis***, –, New Zealand, PDD107704, KT875184, in ITS, MH141043, MH141026; ***C. memoria-annae*** Gasparini, –, Australia, HO529024, EU660945, –, –, –; ***C. microspermus*** J.E.Lange, *Microspermi*, Belgium, DB4657, **ON832640**, MK277784, **ON843887**, –; ***C. microspermus***, *Microspermi*, Sweden, IB19850073, UDB001090, –, –, –; ***C. mucosus*** (Bull.) J.Kickx f., *Myxacium*, Canada, SMI264, FJ039581, in ITS, –, –; ***C. multiformis*** Fr., *Multiformes*, Canada, F16414, FJ039635, in ITS, –, –; ***C. ochroamarus*** Niskanen, Kytöv. & Liimat., *Vibratiles*, Finland, TN04-761 [holotype], KR011132, –, –, –; ***C. ochroamarus***, *Vibratiles*, Estonia, TUF135764, UDB0799615, –, –, –; ***C. olorinatus*** E.Horak, *Olorinati*, New Zealand, PDD72753, HM060330, HM060331, –, –; ***C. olorinatus***, *Olorinati*, New Zealand, PDD87767, MT056036, MT056032, MZ727579, MZ727574; ***C. papulosus*** Fr., *Elastici*, Germany, TUB011867, AY669555, in ITS, KJ403777, –; ***C. periclymenus*** Soop, –, New Zealand, PDD71008 [holotype], GU233351, GU233379, –, MZ727575; ***C. picoides*** Soop, *Turmales*, New Zealand, PDD103886, KF727380, KF727302, –, –; ***C.*** cf. ***picoides***, *Turmales*, New Caledonia, PGK13-126, KY774178, –, –, –; ***C. pinguis*** (Zeller) Peintner & M.M.Moser, *Myxacium*, Canada, F17137, GQ159880, in ITS, –, –; ***C. pluviorum*** Jul.Schäff. ex M.M.Moser, *Microspermi*, Canada, F16068, FJ157038, in ITS, –, –; ***C. pluviorum***, *Microspermi*, Canada, PK5640, HQ604684, in ITS, –, –; ***C.*** aff. ***pluvius*** coll., *Vibratiles*, U.S.A., CLC1762, **ON832641**, **ON832648**, **ON843888**, **ON843891**; ***C.*** aff. ***pluvius*** coll., *Vibratiles*, Canada, DAVFP 26186, EU821695, in ITS, –, –; ***C.*** aff. ***pluvius*** coll., *Vibratiles*, Canada, DAVFP 26240, EU821696, in ITS, –, –; ***C.*** aff. ***pluvius*** coll., *Vibratiles*, Canada, ANT279-HRL2132, MN992353, **ON832649**, –, **ON843892**; ***C.*** aff. ***pluvius*** coll., *Vibratiles*, Canada, MQ18R448-QFB30964, MN751442, **ON832650**, –, **ON843893**; ***C. populinus*** Brandrud, *Phlegmacium*, Norway, O-F-58647, AY669521, in ITS, –, –; ***C. porphyroideus*** Peintner & M.M.Moser, *Dulciolentes*, New Zealand, PDD106018, MH101579, MH108417, MH141031, –; ***C. pseudotriumphans*** M.M.Moser & E.Horak, *Alboaggregati*, Argentina, CT4381, KY462356, –, –, –; ***C. pseudotriumphans***, *Alboaggregati*, Argentina, TUB011873, AY669600, in ITS, KJ403825, –; ***C. psilomorphus*** Soop, *Vibratiles*, New Zealand, PDD103885 [holotype], KF727393, KF727347, MZ727580, MZ727576; ***C. quaresimalis*** Gasparini, –, Australia, HO522430, AY669616, in ITS, KJ403812, –; ***C. rotundisporus*** Cleland & Cheel, *Delibuti*, Australia, PERTH 05255074, AY669612, in ITS, –, –; ***C. saginus*** (Fr.) Fr., *Phlegmacium*, Germany, TUB011419, AY174797, in ITS, KJ403815, –; ***C. salor*** Fr., *Delibuti*, Germany, TUB011838, AY669592, in ITS, KJ403780, –; ***C.*** cf. ***sclerophyllorum*** II, Austrorapacei, New Zealand, PDD95818, MH101548, MH108387, –, –; ***C. seidliae*** Ammirati, Niskanen & Liimat., *Defibulati*, U.S.A., F17116 [holotype], KR011125, in ITS, –, –; ***C.* sp. 1**, *Vibratiles*, New Caledonia, PGK13-070, KY774174, –, –, –; ***C.* sp. 2**, *Vibratiles*, Canada, MQ18R097-QFB30613, MN751578, –, –, **ON843896**; ***C.* sp. 2**, *Vibratiles*, Canada, MQ18R283-QFB30799, MN751579, **ON832652**, –, **ON843897**; ***C.* sp. 3**, *Microspermi*, New Caledonia, CM13-193, KY774143, –, –, –; ***C.* sp. 4**, Electridii, New Caledonia, CY13-068, KY774093, –, –, –; ***C. stillatitius*** Fr., *Defibulati*, Germany, TUB011587, AY669589, in ITS, KJ403835, –; ***C. talus*** Fr., *Multiformes*, Germany, TUB011877, AY669530, in ITS, KJ403793, –; ***C. taylorianus*** E.Horak, *Archeriani*, New Zealand, PDD107692, MH101581, MH108419, –, –; ***C. taylorianus***, *Archeriani*, New Zealand, PDD27259 [holotype], MT363110, –, –, –; ***C. tenuipes*** (Hongo) Hongo, *Turmales*, Japan, AB301613, AB301613, –, –, –; ***C. triumphans*** Fr., –, Germany, TUB011461, AY174799, in ITS, –, –; ***C. trivialis*** J.E.Lange, *Myxacium*, Germany, TUB020404, KJ421158, in ITS, –, –; ***C. turcopes*** Soop, *Turcopedes*, New Zealand, PDD94051 [holotype], JQ287697, –, –; ***C. turcopes***, *Turcopedes*, New Zealand, PDD94058, JQ287700, MK277872, –, –; ***C. turmalis*** Fr., *Turmales*, Germany, TUB011393, AY174782, in ITS, KJ403822, –; ***C. vanduzerensis*** A.H.Sm. & Trappe, *Defibulati*,

Appendix 1. Continued.

Canada, VMS28, FJ717562, in ITS, –, –; ***C. variecolor*** (Pers.) Fr., *Phlegmacioides*, Germany, TUB011416, AY174795, in ITS, EU088239, –; ***C. variegatus*** Bres., –, Germany, TUB019764, KJ421003, in ITS, KJ403806, –; ***C. vibratilis*** (Fr.) Fr., *Vibratiles*, Hungary, DB2020-10-24-1, **ON832641**, **ON832653**, **ON843889**, –; ***C. vibratilis***, *Vibratiles*, Finland, H6031329 [neotype], MZ568649, –, –, –; ***C.*** cf. ***vibratilis*** I, *Vibratiles*, Canada, F16046, FJ157098, in ITS, –, –; ***C.*** cf. ***vibratilis*** I, *Vibratiles*, Norway, M4, KC842440, KC842510, –, –; ***C.*** cf. ***vibratilis*** I, *Vibratiles*, Norway, MP-C12-18, **ON832632**, –, –, –; ***C.*** cf. ***vibratilis*** II, *Vibratiles*, Canada, DAVFP 26530, EU821694, in ITS, –, –; ***C.*** cf. ***vibratilis*** III, *Vibratiles*, U.S.A., SLB2003101209, FJ717578, in ITS, –, –; ***C.*** aff. ***vibratilis***, –, Canada, ANT294-QFB28822, MN992358, –, –, **ON843894**; ***C.*** aff. ***vibratilis***, –, Canada, MQ18-HL1300-QFB30038, MN751577, **ON832651**, –, **ON843895**; ***C.*** aff. ***vibratilis***, –, Romania, C188, ON832643, –, –, –; ***C. viscostriatus*** E.Horak, *Turcopedes*, New Zealand, PDD27272 [holotype], GU233335, –, –, –; ***C. viscostriatus***, *Turcopedes*, New Zealand, PDD97513, KJ635235, in ITS, –, –; ***C. vitreofulvus*** Soop, *Marmorati*, New Zealand, PDD97545 [holotype], KJ635243, in ITS, MH141036, MH141018; ***C.*** cf. ***xenosma***, *Olorinati*, New Zealand, OTA60162, JX178619, MZ723314, MZ727577, MZ727572.